TWO NEW SPECIES FROM THE BREVANTHERUM CLADE OF SOLANUM (SOLANACEAE) FROM EASTERN BRAZIL

Leandro L. Giacomin

Departamento de Botânica Instituto de Ciências Biológicas Universidade Federal de Minas Gerais Av. Antônio Carlos, 6627, 31270-901 Belo Horizonte, MG, BRAZIL giacomin.leandro@gmail.com

Lynn Bohs

Department of Biology
University of Utah
257 South 1400 East
Salt Lake City, Utah 84112-0840, U.S.A.

João R. Stehmann

Departamento de Botânica Instituto de Ciências Biológicas Universidade Federal de Minas Gerais Av. Antônio Carlos, 6627, 31270-901 Belo Horizonte, MG, BRAZIL

ABSTRACT

Two new species of Solanum (Solanaceae) from eastern Brazil are described. Solanum anisocladum Giacomin & Stehmann is similar to S. megalochiton Mart., but differs by the indument of the adaxial leaf surface, which is composed of long porrect-stellate and unbranched trichomes. It also has a more robust habit and a unique branching pattern of the flowering stems. It is restricted to the Atlantic Rainforest of northeastern Brazil and was previously misidentified as S. megalochiton. The other species, Solanum caelicolum Giacomin & Stehmann, is endemic to Espírito Santo state and is most similar to S. hirtellum (Spreng.) Hassl., but differs mainly by its adaxial leaf indument, with porrect-stellate trichomes with a central ray smaller than the lateral ones, by its comparatively larger fruiting calyx that can reach up to three times the diameter of the mature berry and by its sessile to subsessile unbranched congested inflorescence. Both species belong to the Brevantherum clade, one of the main lineages identified in the genus Solanum, and are placed together in a clade which contains species from S. sects. Extensum D'Arcy and Stellatigeminatum Child. Complete descriptions, distributions, and preliminary conservation assessments of the new species are given.

RESUMO

Duas novas espécies de *Solanum* (Solanaceae) são descritas para o leste do Brasil. **Solanum anisocladum** Giacomin & Stehmann é semelhante a *S. megalochiton* Mart., mas difere pelo indumento observado na face adaxial de suas folhas, composto por longos tricomas porrecto-estrelados associados a tricomas não ramificados, além de um hábito mais robusto, bem como um padrão de ramificação inusitado. A espécie é restrita às formações ombrófilas da Floresta Atlântica do nordeste do Brasil, e foi erroneamente determinada como *S. megalochiton*. A outra espécie, **Solanum caelicolum** Giacomin & Stehmann é endêmica do estado do Espírito Santo e é semelhante a *S. hirtellum* (Spreng.) Hassl. mas difere desta por seu indumento da face adaxial das folhas composto por tricomas porrecto-estrelados de raio central mais curto que os laterais, por seus lobos do cálice comparativamente mais longos, que podem atingir até três vezes o diâmetro do fruto maduro e por sua inflorescência não ramificada, congesta, séssil a subséssil. Ambas as espécies pertencem ao clado Brevantherum, uma das principais linhagens definidas para o gênero *Solanum*, e podem ser alocadas junto a um subclado que contém espécies das seções *Extensum* D'Arcy e *Stellatigeminatum* Child. Descrições completas, distribuições geográficas conhecidas e categoria de ameaça das espécies são apresentadas.

INTRODUCTION

Solanum L. (Solanaceae) is among the largest genera of flowering plants and contains approximately 1500 species with a worldwide distribution. Since 2004, it has been focus of a comprehensive species-level taxonomic inventory aiming to provide online descriptions of all its species (the PBI Solanum project; Knapp et al. 2004; http://www.solanaceaesource.org). This collaborative effort has led to the discovery of several new taxa from different countries (e.g., Peralta et al. 2005; Granados-Tochoy & Orozco 2006; Knapp 2007; Knapp & Nee 2009; Nee et al. 2006; Stern & Bohs 2009; Tepe & Bohs 2009; Knapp 2010a & b; Farruggia & Bohs 2011; Giacomin & Stehmann 2011; Vorontsova & Knapp 2012). The project was coincidentally developed together with

a large-scale initiative in Brazil to achieve the Target 1 of the Global Strategy for Plant Conservation adopted by the parties to the Convention on Biological Diversity (CBD) in 2002: the construction of a working list of the plant species for the country (Forzza et al. 2010). The construction of the Brazilian list of Solanaceae (Stehmann et al. 2010) revealed several poorly known or unknown taxa, and two of these are described here.

Previous molecular phylogenetic studies have identified the Brevantherum clade as one of the 12 to 15 main lineages of Solanum (Bohs 2005; Weese & Bohs 2007). This clade has been target of intensive studies by the authors in order to better understand the evolution of the group and the relationships among its species. It has a New World distribution, occurring from the southern United States through Argentina, with a center of diversity in Brazil. It comprises unarmed herbs to shrubs with unbranched to variously branched and stellate trichomes encompassing at least six sections treated in past classification systems. Molecular data have identified two subclades within the Brevantherum clade (see Weese & Bohs 2007 for more details). The first subclade comprises members of S. sect. Gonatotrichum Bitter, which are herbs to shrubs, mainly with an indument of unbranched trichomes (except for S. lignescens Fernald), and are easily characterized by the explosive dehiscence of their fruits (Stern & Bohs 2012; Stern et al. 2013). The other subclade contains species from five sections treated in past classifications (sects. Brevantherum Seithe, Cernuum Carvalho & Sheph., Extensum D'Arcy, Lepidotum Seithe and Stellatigeminatum Child), and all share branched to stellate or peltate hairs as a main character. Molecular phylogenies based on three gene regions (nuclear ITS and GBSSI and plastid trnT-F) indicate that Solanum sect. Brevantherum is largely monophyletic (L. Giacomin et al., unpub. data), but the monophyly of the other four sections has not been established and the relationships among them are uncertain. The limits of these sections are not well demarcated and they are in dire need of a revision, as pointed out by other authors (Child 1998; Nee 1999).

Although most recent classification systems place species with lepidote scales in *Solanum* sect. *Lepidotum* and species with large leaves and usually bristly-pubescent or scaly inflorescence axes in sect. *Cernuum*, there is no similar consensus about the characters defining *S.* sects. *Extensum* and *Stellatigeminatum* (Child 1998; Nee 1999). Child (1998) proposed that the concept of *S.* sect. *Extensum* should be applied only to climbing or sprawling species from Central America with somewhat foliaceous calyces and plurifoliate sympodia, even though the protologue for *S.* sect. *Extensum* did not list the sympodial structure as diagnostic (D'Arcy 1972). The species from South America with foliaceous calyces (a diagnostic character cited by D'Arcy, 1972), but with difoliate-geminate sympodial units were placed in *S.* sect. *Stellatigeminatum* by Child (1998). Nee (1999) disagreed with this proposition and, like D'Arcy (1972), included the species with foliaceous accrescent calyces and fasciculate axillary inflorescences in sect. *Extensum*. The entire Brevantherum clade is currently under investigation by the authors in order to better understand its infrageneric groupings.

While sampling the species of the Brevantherum clade from Brazil for phylogenetic studies, an undescribed species was revealed from Espírito Santo state. Also, while reevaluating the species limits of Solanum megalochiton Mart. from the northeast, a new segregate species was discovered. The new species do not have lepidote scales or scaly inflorescence axes, and are expected to belong to the undefined mixed clade to which the type species of sections Extensum and Stellatigeminatum are assigned.

MATERIALS AND METHODS

Material from the following herbaria was reviewed (acronyms from Index Herbariorum, http://sweetgum.nybg.org/ih/): BHCB, CEPEC, EAC, HUEFS, IPA, MG, MBML, PEUFR, RB and UFP, as well as the non-indexed HST at Recife, Brazil. Images of types were accessed through JSTOR Plant Science (http://plants.jstor.org) or collections websites from BM, F, G, M and P. We assessed the conservation status using IUCN Red List Categories and Criteria (IUCN 2010) and for the extent of occurrence calculation a minimum convex polygon (MCP) was used within ArcGIS software (ESRI). The terminology used to describe the vestiture and trichome types was based on Roe (1971) and Mentz et al. (2000). The delimitation of the new taxa was based on a morphological species concept where the species is recognized as distinct if possessing a unique suite of characters and separated from its similar species by morphological gaps (Mallet 1995).

RESULTS

TAXONOMIC TREATMENT

Solanum anisocladum Giacomin & Stehmann, sp. nov. (Figs. 1, 2A–F, 3A–D). Type: BRASIL. Pernambuco: Mun. Jaqueira, RPPN Frei Caneca, Serra do Urubu, trilha da Mata da Caranha, topo da serra, 08°42'52.5"S, 35°50'54"W, 700 m, 31 Mar 2012 (fl, fr), L.L. Giacomin et al. 1794 (HOLOTYPE: BHCB [BHCB002730]; ISOTYPES: NY, RB, UFP, UT).

Solanum anisocladum differs from Solanum megalochiton Martius by its more robust habit tending to form small trees up to 5 m with a prominent trunk, while S. megalochiton is mostly a shrub up to 3 m branched from near the base; its hirsute indument mainly composed of long trichomes (up to 2.6 mm; Fig. 2A–B), with the older stems becoming hispid due to the remnants of the stalks of the stellate trichomes (observed both in fresh and dried specimens), these mostly soft and up to 1.5 mm in S. megalochiton; the always shiny adaxial leaf suface, even in dry material, with a vestiture of unbranched (Fig. 2D), porrect-stellate, and always eglandular hairs, vs. adaxial leaf surfaces dull, with stellate and frequently glandular hairs in S. megalochiton; and by its unusual branching, with a strong change in stem growth direction where the inflorescence arises between the nodes, whereas S. megalochiton has straight branches.

Shrubs to small trees up to 5 m, usually with a prominent trunk, branching in the upper stems, these spreading. Young stems moderately to densely hirsute to hispid with few-rayed (4-6) porrect-stellate trichomes, these sometimes multangulate, on multiseriate stalks 0.3-1.2 mm long, the rays 0.2-0.8 mm, usually with a 2-3-celled central ray longer than the 1-celled lateral ones; old growth glabrescent to pubescent, usually with broken trichomes comprising a hispid vestiture of multiseriate stalk remnants. Bark of older stems yellowishwhite, usually shiny; new growth whitish-green to dark purple near the insertion of the inflorescence, always shiny. Sympodial units usually trifoliate, rarely di- or plurifoliate, often with solitary leaves; if geminate, leaves paired only at branching points and differing mainly in size, the smaller up to 1/3 the size of the larger ones. Leaves simple, the blades 1.7-11.8(-13) cm long, 1.2-4.8 cm wide, narrowly elliptic to ovate-elliptic, membranaceous, weakly discolorous (dark shiny green above, pale green beneath when fresh), the abaxial surfaces moderately to densely hirsute, the lamina always visible, with short- (more often on the lamina) to long-stalked (more often on primary and secondary veins) porrect-stellate trichomes with 3-5 lateral rays supported by a multiseriate stalk 0.3-0.9(-1.4) mm and a 2-3 celled central ray somewhat longer than the lateral ones (Fig. 2B), 0.8-1.2 mm long, the adaxial surfaces moderately to densely hirsute, the lamina always visible, with mixed hyaline unbranched trichomes (Fig. 2D) up to 1.8 mm long, and sessile (more often on the lamina) to short-stalked (more often on primary and secondary veins) multangulate-stellate trichomes, frequently with few (1-4; Fig. 2C) lateral rays and a 2-3-celled central ray much longer than the others, 0.8-2 mm long and supported by a multiseriate stalk up to 0.4 mm long; venation camptodromous, impressed or not above (barely visible in dried material), raised beneath, the secondary veins 5-9 pairs; base rounded to cuneate, asymmetric; margins entire, slightly revolute; apex acute to long attenuate-caudate (only acute on the smaller geminate leaves); petioles 1.8-5.5 mm long, densely hirsute, with the same trichomes as those of the abaxial midrib. Inflorescence an elongated unbranched cyme, terminal, lateral, internodal, or subopposite the leaves, when internodal, changing the orientation of the branch (see comments; Figs. 1, 3A-B), the axes (0.35-)0.9-4.3 cm long, with (3-)6-15 flowers, subsessile to pedunculate, the peduncles 0.1-1.47 cm long, moderately hirsute with porrect-stellate trichomes like those of the stems, the rachis pale green, densely pubescent with three types of trichomes: hyaline, unbranched, 2-4-celled, eglandular or glandular-capitate trichomes, sessile to short-stalked multangulate-stellate trichomes with few (1-4) lateral rays or only the 2-4-celled, sometimes glandular-capitate central ray developed, this much longer than the others, and supported by a multiseriate stalk up to 0.4 mm long, and long-stalked porrect-stellate trichomes like those of the peduncle with stalks up to 0.9 mm long; pedicels 0.3-1.2 cm long in flower, 1.9-2.5 cm in fruit, pale green to dark pink to purplish at base, articulated at base, 1 mm in diameter at base, densely pubescent with the same unbranched trichomes found on the rachis, almost all with a glandular head, up to 2 mm long, mixed with sessile to short-stalked multangulate trichomes with 1-4 lateral rays and a longer central ray. Buds slightly elongated with developed calyx lobes, the corolla nearly included even when fully developed. Flowers perfect, 5-merous. Calyx tube 1-2 mm long, with lanceolate to narrow-ovate lobes 6-8 mm long, 3-4 mm wide in flower, the apices acuminate, strongly accrescent in fruit, the lobes broadly ovate to cordate, 8.6-12 mm long, 8-10 mm wide, the apices acute, densely covered abaxially with the same trichome types of the rachis, but the porrect-stellate hairs with



Fig. 1. Holotype of Solanum anisocladum Giacomin & Stehmann. (L.L. Giacomin et al. 1794, BHCB [BHCB002730]). Specimen image reproduced with the permission of the BHCB Herbarium, Departamento de Botânica, ICB, Universidade Federal de Minas Gerais.

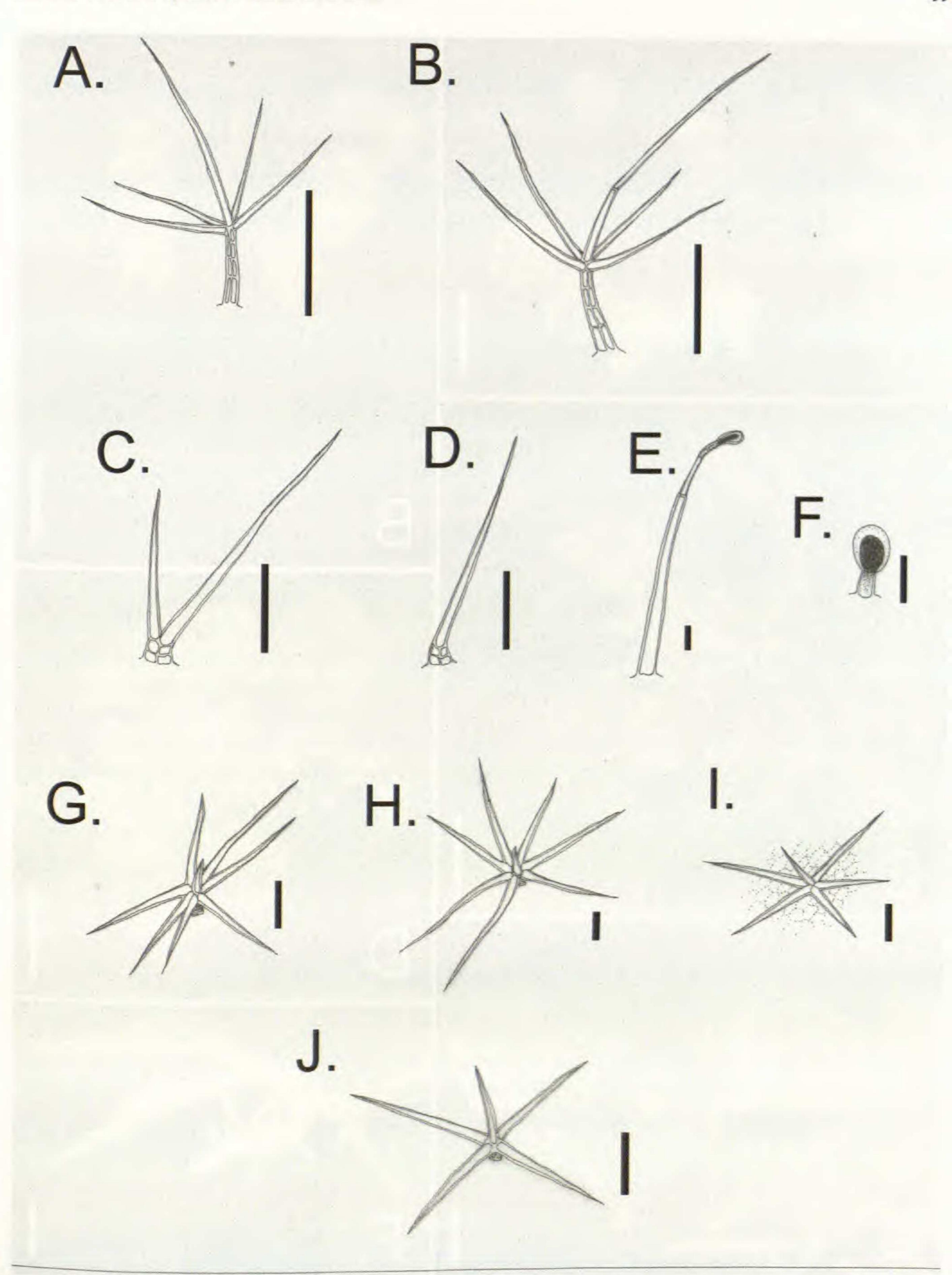


Fig. 2. Hair types of A—F: Solanum anisocladum Giacomin & Stehmann [all from L.L. Giacomin et al. 1794 (BHCB)]. A. Porrect-stellate hair of the stem. B. Porrect-stellate long-stalked hair of the abaxial leaf surface. C. Furcate hair of the adaxial leaf surface. D. Unbranched hair with a multicellular base of the adaxial leaf surface. E. Multicellular unbranched glandular capitate hair with an ellipsoid glandule of the adaxial calyx surface. F. Glandular globose hair on adaxial calyx surface. G—J: Solanum caelicolum Giacomin & Stehmann [G—I from V. Demuner et al. 4253 (BHCB), J from V. Demuner et al. 3273 (BHCB)]. G. Porrect-stellate short-stalked hair from stem. H. Porrect-stellate hair with a very reduced midpoint from abaxial leaf surface. I. Porrect-stellate sessile hair from adaxial leaf surface. J. Porrect-stellate hair with a subequal rays from adaxial calyx surface. Scale bars: A—D = 500 μm; E—J = 100 μm.

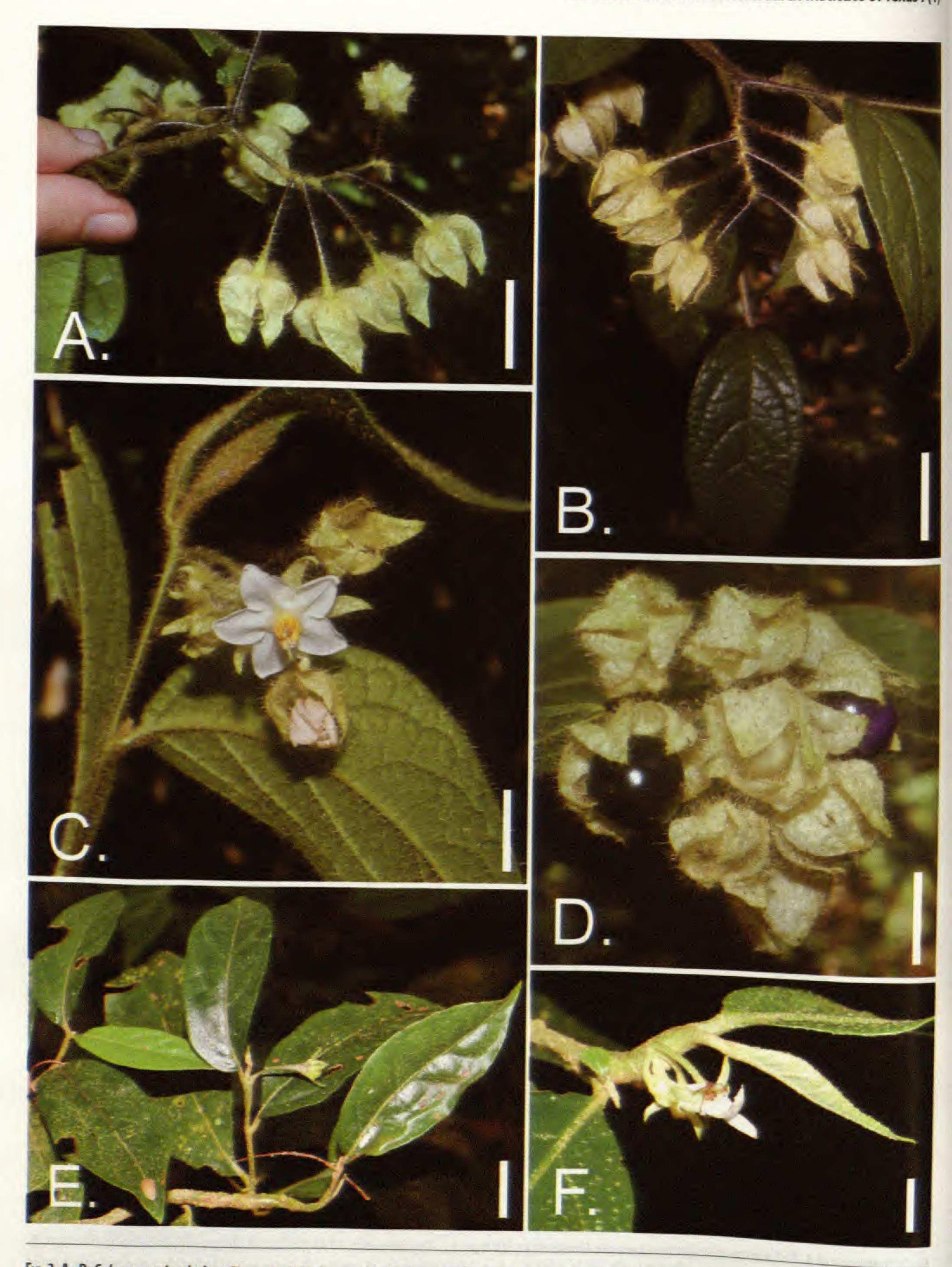


Fig. 3. A—D: Solanum anisocladum Giacomin & Stehmann [field pictures of L.L. Giacomin et al. 1794 (BHCB)]. A. The unusual branching pattern diagnostic of S. anisocladum Giacomin & Stehmann (see comments). B. The robust inflorescence and the change in branch direction where the inflorescence arises near the leaf. C. Stellate spreading corolla and calyx. D. Mature fruit. E—F: Solanum caelicolum Giacomin & Stehmann [field pictures of L.L. Giacomin et al. 1852 (BHCB)]. E. Immature fruit. F. Congested sessile cyme. Scale bars: A—C and E = 1 cm; D = 1.5 cm; F = 0.5 cm.

shorter stalks and the central ray always longer than the others and often glandular, adaxially with unbranched 2–4-celled (sometimes with a poorly developed secondary ray) glandular capitate trichomes up to 2 mm long (Fig. 2E), the gland ellipsoidal, these commonly found also on the margin, associated with sessile to subsessile globose dark glandular trichomes (Fig. 2F), these concentrated on the midveins and near the base. Corolla 1.3–1.7 cm in diameter, white, stellate, lobed up to ¾ to the base, the lobes 4–6 mm long, 4.5–6.5 mm wide, deltoid to ovate, with acute, slightly involute apices, spreading at anthesis, sparsely to moderately pubescent abaxially with the same trichome types found adaxially on the calyx and with a tuft of small unbranched eglandular trichomes at apex, glabrous adaxially. Filament tube up to 1 mm long, with a minute free portion less than 1 mm long, glabrous; anthers 2.8–4 mm long, 1.3–1.5 mm wide, sometimes slightly unequal, elliptic to oblong, connivent, yellow, glabrous on both faces, poricidal at apex, with the pores directed introrsely, opening into longitudinal slits with age. Ovary glabrous; style 6–7 mm long, cylindrical; stigma clavate, with a papillose surface. Fruit a globose berry 1–1.4 cm in diameter, white to pale green when immature, purple to black when mature, shiny, glabrous, drying brown to dark, completely covered by the accrescent calyx which spreads open at maturity. Seeds 9–31(–35) per fruit, 2.3–3.4 mm long, 1.7–2.3 mm wide, flattened, reniform, golden to brown, the surfaces with irregular pits.

Additional specimens examined. **BRASIL. Alagoas:** Mun. Murici, Poço D'Anta, ca. 16–19 km NNW of Murici by road, Mata de Murici, 9°13.53'S, 35°52.776'W, 550–600 m, 14 May 2001 (fl, fr), W.W. Thomas et al. 12441 (BHCB, NY, RB). **Bahia:** Mun. Ibirapitanga, Faz. Paineiras, 17 Feb 1998 (fl, fr), A.S. Conceição 213 (MG). **Pernambuco:** Mun. Maraial/Lagoa dos Gatos, Serra do Urubu, 20 Apr 1994 (fl, fr), A.M. Miranda & L.P. Felix 1628 (EAC, HST).

Discussion.—Solanum anisocladum is a species with a robust habit, forming small trees up to 5 m tall with prominent trunks, with the upper leaf surface shiny, dark green, and drying dark. It is similar to Solanum megalochiton which normally forms much branched shrubs up to 3 m tall, with the surface matte, often covered by a whitish-yellow indument, and normally pale green when dried. Both species share an inflated calyx that is strongly accrescent at fruit maturity (Fig. 3D). This feature was previously used to separate S. megalochiton from similar species such as S. didymum Dunal. However, S. anisocladum presents several other characters that readily distinguish it from S. megalochiton. Its indument of very long stellate and unbranched hairs reaching more than 2 mm long and drying ferruginous (Figs. 1, 2A-B) is easily visible to the naked eye. The old growth becomes somewhat hirsute to hispid where only the multiseriate stalks of the stellate trichomes remain. The indument in S. megalochiton is much softer, reaches up to 1.5 mm long, is normally transparent to yellowish when dried, and the stems never become hispid. The inflorescence is also a distinctively robust unbranched cyme (Fig. 3A-B), sometimes with an axis reaching more than 4 cm long, whereas the inflorescences of S. megalochiton are normally shorter than 2.5 cm. Its adaxial leaf indument is composed of eglandular porrectstellate trichomes associated with unbranched hairs, the latter with multicellular bases, apparently representing stellate hairs without developed lateral rays. The adaxial leaf indument of S. megalochiton is composed only of stellate hairs, these sometimes glandular. Solanum anisocladum also has a distinctive branching pattern not observed in S. megalochiton (Fig. 3A). When arising from between the nodes, the inflorescences can invoke a strong change in growth direction (not always visible on small branches in herbarium sheets, but observed in every specimen seen at the field). In contrast, the flowering branches of S. megalochiton are more or less straight.

In the Brazilian plant species list (Stehmann et al. 2010), Solanum megalochiton was cited as occurring in northeastern Brazil from the states of Alagoas and Bahia. During visits to herbaria in Pernambuco and Bahia no specimens matching it were seen co-occurring with *S. anisocladum*. A sheet from Alagoas (*Thomas 12441*; BHCB, NY, RB) determined as *S. megalochiton* by other *Solanum* experts actually conforms to our concept of *S. anisocladum*. Thus, in northeastern Brazil, *S. megalochiton* is known to occur only in a few locations in the wet forests of the southern part of Bahia and not further northward. *Solanum megalochiton* can also be found in all states of the southeastern and southern regions of Brazil, with a few additional collections in the state of Goiás and Mato Grosso. This suggests that *S. anisocladum* and *S. megalochiton* are not sympatric, but this cannot be confirmed because not all important collections of the group from the northeast have been seen at present (e.g., JPB).

Etymology.—The name Solanum anisocladum was given because of the peculiar branching pattern resulting in unequal branches when the inflorescence arises from between the nodes.

Distribution and habitat.—Solanum anisocladum occurs in forest edges of the Atlantic coastal rainforest of northeastern Brazil in the states of Alagoas, Bahia, and Pernambuco, in partial to complete shade, at elevations of 500–700 m (Fig. 4). Primary wet forest fragments at this elevation are quite rare in northeastern Brazil today, and the type collection, despite the fact that it was found in a forest edge, was from a well preserved fragment.

Phenology.—The species was collected with flowers and fruits from February through May, but a flowering peak was observed in February and March, and fully developed fruits were found from March through May.

Preliminary conservation status.—Endangered B1 a,b (i, ii, iii, iv). Solanum anisocladum is known from only three localities and its calculated extent of occurrence using the MCP is 834 km². Despite the fact that the Bahia registry is far from the one in Pernambuco state, the MCP reflects the narrow range of coastal rainforest where the species is expected to occur. Although the type locality is now part of a private reserve owned by a sugar company (RPPN Frei Caneca), it consists of a small group of forest fragments in a severely damaged landscape mainly modified by extensive agriculture based on monoculture (plantations). Generally, the Atlantic coastal rainforest has been severely damaged in northeastern Brazil in the past decades due to urban expansion and extensive farming.

Solanum caelicolum Giacomin & Stehmann, sp. nov. (Figs. 2G–J, 3E–F, 5). Type: BRASIL. Espírito Santo: Colatina, Alto Moacir, Prop.: Lalau (property of Sr. Landislau), 19°29'37"S, 40°33'08"W, 200 m, 20 Mar 2007 (fl, fr), V. Demuner et al. 3273 (HOLOTYPE: MBML; ISOTYPE: BHCB [BHCB002734]).

Differs from Solanum hirtellum (Spreng.) Hassl. by its adaxial leaf and calyx indument, with porrect-stellate trichomes always with a one-celled central ray much smaller than the lateral ones; in S. hirtellum the central ray of the stellae on adaxial leaf surfaces is mostly longer than the lateral rays. Solanum caelicolum also differs in its sessile to subsessile congested inflorescences that are much shorter and never branched (Fig. 3F), with the pedicels arising very close to each other, in contrast to the pedunculate, lax (the pedicels well-separated from each other), sometimes several-branched inflorescences of S. hirtellum. Solanum caelicolum has a comparatively larger calyx, with the lobes reaching up to three times the fruit diameter at maturity; the calyx lobes in S. hirtellum are not larger than the berry at maturity.

Shrubs, up to 3 m, sometimes scandent, much branched, the apical branches scandent, held downwards, arching. Young stems densely pubescent with sessile to short-stalked porrect-stellate trichomes normally with 8 lateral rays, rarely fewer, commonly of unequal length, up to 0.3 mm long, with a central ray much shorter than the lateral ones (Fig. 2G); old growth sparsely pubescent to glabrescent. Bark of older stems bright white to yellowish, shiny; new growth gray due to dense vestiture, with a white to dark purple lamina beneath. Sympodial units 2-3 foliate, geminate, with paired leaves differing in size and shape, the smaller ones less than 1/4 of the size of the larger. Leaves simple, the blades 2.2-7 cm long, 1-3 cm wide, elliptic to broadly elliptic (the smaller geminate leaves broadly elliptic to ovate, sometimes slightly obovate), membranaceous to chartaceous, slightly discolorous, drying dark adaxially, the abaxial surfaces sparsely to moderately pubescent, the pubescence denser on veins, with sessile to short-stalked porrect-stellate trichomes with 4-9 lateral rays up to 0.3 mm long, frequently unequal in length, and a minute central ray (Fig. 2H), always shorter than the laterals, up to 0.1 mm long, the stalks multiseriate, reaching 0.1 mm long, the adaxial surfaces glabrescent, with hairs only on the veins or sparsely pubescent on the lamina, with sessile porrect-stellate trichomes with 4-8 lateral rays (trichomes observed on veins frequently more rayed), up to 0.3 mm long, frequently unequal, with a slightly longer central ray than on the abaxial surface (Fig. 21), reaching 0.2 mm long, but still shorter than the lateral ones; venation camptodromous, slightly to not raised above, raised beneath, the secondary veins 4-6 pairs; base cuneate to obtuse (rounded on the smaller geminate leaves), asymmetric; margins entire, plane; apex long-attenuate to acuminate (obtuse to rounded on the smaller geminate leaves); petioles 2.3-5 mm long, densely pubescent with the same trichomes as the stem and abaxial midrib. Inflorescence a congested unbranched cyme, lateral, internodal, or subopposite the leaves, rarely terminal, the axis sessile to subsessile, up to 3 mm long, the peduncle up to 1 mm or absent, green, moderately to densely covered with the same porrect stellate trichomes as the stem, the rachis barely visible to absent, with the pedicels very closely spaced; pedicels



Fig. 4. Known distribution of Solanum anisocladum (circles) and S. caelicolum (triangles) in eastern Brazil.



Fig. 5. Isotype of *Solanum caelicolum* Giacomin & Stehmann. (V. Demuner et al. 3273, BHCB [BHCB 002734]). Specimen image reproduced with the permission of the BHCB Herbarium, Departamento de Botânica, ICB, Universidade Federal de Minas Gerais.

3-8 mm long in flower, 5-9 mm in fruit, green at base, becoming purplish distally, articulated at base, less than 1 mm in diameter at base, moderately to densely pubescent with sessile to subsessile porrect-stellate trichomes with up to 8 lateral rays, the central ray much shorter than the others, and sometimes with 3-4 celled uniseriate glandular hairs near the calyx. Buds globose, the corolla emergent from the calyx lobes, spreading just before anthesis. Flowers perfect, 5-merous. Calyx tube up to 1 mm long, with narrow oblong to lanceolate lobes 1.6-2.5 mm long, 0.7-1 mm wide in flower, 2.5-3 mm long, 1-1.2 mm wide in fruit, with acute to acuminate apices, becoming ovate, accrescent, but not covering the whole mature berry, covered abaxially with the same porrect-stellate trichomes found on the pedicels, associated with unbranched 3-4-celled glandular capitate trichomes, barely visible in dried material, adaxially with sparse porrect-stellate trichomes, smaller than those found abaxially, with 4-7 lateral rays, often the same size as the central ray (Fig. 2J), associated with unbranched glandular capitate trichomes at the base near the ovary, and also with a tuft of unbranched eglandular trichomes at the calyx lobe apices. Corolla 0.8-1 cm in diameter, white, stellate, lobed up to ¾ its length, the lobes 3.2-3.8 mm long, 1.8-2.2 mm wide, ovate to elliptic, with acute to acuminate apices, spreading at anthesis, moderately pubescent abaxially with the same porrect-stellate trichomes as the adaxial calyx surface, with a central ray the same size or sometimes longer than the lateral ones, associated with minute one-celled unbranched or sometimes forked, sometimes glandular hairs densely covering the margins, glabrous adaxially. Filament tube up to 0.5 mm, with a free portion reaching 0.6 mm, sometimes slightly unequal, glabrous; anthers 1.6-2 mm long, 0.7-1 mm wide, elliptic, connivent, yellow, glabrous abaxially, with unbranched, forked, or sometimes stellate eglandular trichomes adaxially, these erect or mostly lying flat, pointing upwards, poricidal at apex, the pores directed introrsely, opening into longitudinal slits with age. Ovary glabrous; style 1.8-3 mm long, stigma cylindrical, slightly clavate, with a papillose surface. Fruit a globose berry, 0.7-0.9 cm in diameter, white to pale green when immature, purple at maturity, shiny, glabrous, drying brown to dark, initially covered by the accrescent calyx that spreads at maturity. Seeds few (2-3 observed in mature fruits), 2.5-3 mm long, 2-2.4 mm wide, flattened, reniform, pale brown, the surface with irregular pits.

Additional specimens examined. **BRASIL. Espírito Santo**: Mun. Marilândia, Liberdade, Água Viva, Pedra do Cruzeiro, prop.: Aguilar A. Lorencini, 19°20'53.7"S, 40°33'03.6"W, 150 m, 19 Jan 2006 (fl, fr), *V. Demuner et al.* 1697 (MBML); same locality, 19°20'45"S, 40°32'57"W, 300 m, 13 Jun 2007 (fr), *V. Demuner et al.* 4253 (BHCB, MBML); Mun. Santa Teresa, Comunidade de Santo Antônio, propriedade do Sr. Boza, fragmento de floresta ombrófila densa, após plantação de eucalipto, à direita da entrada, descendo o vale, 19°54'32.3'S, 40°35'25.6"W, 740 m, Fragmento de floresta ombrófila densa, após plantação de eucalipto, à direita da entrada, descendo o vale, 19°54'32.3'S, 40°35'25.6"W, 740 m, Fragmento de floresta ombrófila densa, após plantação de eucalipto, à direita da entrada, descendo o vale, 19°54'32.3'S, 40°35'25.6"W, 740 m, Fragmento de floresta ombrófila densa, após plantação de eucalipto, à direita da entrada, descendo o vale, 19°54'32.3'S, 40°35'25.6"W, 740 m, Fragmento de floresta ombrófila densa, após plantação de eucalipto, à direita da entrada, descendo o vale, 19°54'32.3'S, 40°35'25.6"W, 740 m, Fragmento de floresta ombrófila densa, após plantação de eucalipto, à direita da entrada, descendo o vale, 19°54'32.3'S, 40°35'25.6"W, 740 m, Fragmento de floresta ombrófila densa, após plantação de eucalipto, à direita da entrada, descendo o vale, 19°54'32.3'S, 40°35'25.6"W, 740 m, Fragmento de floresta ombrófila densa, após plantação de eucalipto, à direita da entrada, descendo o vale, 19°54'32.3'S, 40°35'25.6"W, 740 m, Fragmento de floresta ombrófila densa, após plantação de eucalipto, à direita da entrada, descendo o vale, 19°54'32.3'S, 40°35'25.6"W, 740 m, Fragmento de floresta ombrófila densa, após plantação de eucalipto, à direita da entrada, descendo o vale, 19°54'32.3'S, 40°35'25.6"W, 740 m, Fragmento de floresta ombrófila densa, após plantação de eucalipto, à direita da entrada, descendo o vale, 19°54'32.3'S, 40°35'25.6"W, 740 m, Fragmento de floresta observada de calibração de eucalipto, à direita da e

Discussion.—Solanum caelicolum resembles S. hirtellum, sharing with it a similar habit and stem indument, leading to misidentifications of collections from Espírito Santo state in the past. It can be distinguished by its elliptic leaves, not ovate like those of S. hirtellum, that are glabrescent and usually drying dark adaxially (normally moderately pubescent and pale green in S. hirtellum), abaxially drying somewhat gray to pale green due to the conspicuous indument (normally inconspicuously pubescent and pale green in S. hirtellum). The adaxial leaf trichomes are also distinct from those of S. hirtellum. While S. caelicolum has porrect-stellate trichomes with a very reduced midpoint (central ray; Fig. 2H), S. hirtellum mostly has stellae with the central ray sometimes multicellular and longer than the lateral rays on the upper leaf surfaces. Some variation in trichome morphology occurs in S. hirtellum, but at least some of the hairs of the adaxial leaf surfaces have a central ray longer than the lateral ones. Solanum caelicolum also has a distinctive sessile to subsessile congested and unbranched inflorescence (Fig. 3F) with the pedicels arising very close to each other (the rachis almost absent), whereas the inflorescence in S. hirtellum is mainly pedunculate, few- to many-branched, and lax, with the pedicels arising up to 0.5 cm from each other. Pedicel size can also be used to distinguish both species; they are up to 8 mm long in S. caelicolum and frequently exceed 8 mm in S. hirtellum. Another good character to distinguish the two species is the size of the fruiting calyx lobes. In S. caelicolum the calyx lobes are larger than the diameter of the mature berry, whereas in S. hirtellum the calyx lobes are shorter than the mature berry.

Both species are known from Espírito Santo state, but they apparently do not co-occur. While S. caeli-colum seems to be restricted to north-central Espírito Santo, S. hirtellum has a much broader distribution, extending from northeast Argentina and Paraguay and reaching its northernmost limit in the south of Espírito Santo.

Etymology.—The epithet caelicolum derives from the Latin "dweller of heaven." It references the region of Santa Teresa and surroundings, where the species was first collected and is most abundant. The region holds a considerable amount of the preserved forest fragments of the Espírito Santo state and plays an essential role in the conservation of the plant species of the Brazilian Atlantic Forest, a severely damaged biome due to human occupation. For Solanum specialists as well as other botanists, it is a heaven of plant diversity and new species.

Distribution and habitat.—Solanum caelicolum inhabits the understory or shaded forest edges of well-preserved fragments of the Brazilian Atlantic coastal rainforest, and is known only from Espírito Santo state from 150 to 850 m (Fig. 4). Despite the fact that the type collection was from an outcrop, the species is believed to inhabit only shaded environments and the reference might be to a granitic boulder in the forest understory, a common situation in Espírito Santo forests.

Phenology.—The species can be found in flower from January through June. Fruits were found from February through June, but fully developed ones were found from March through June.

Preliminary conservation status.—Endangered B1 a,b (i, ii, iii). Solanum caelicolum is known from four localities very close to each other in the state of Espírito Santo, and its calculated extent of occurrence using the MCP is 31 km². At the municipality of Santa Teresa, the locality of three of the collections, there still are several well preserved forest remnants, some of them within protected reserves. One of the collections was found at a city reserve (Estação Biológica de São Lourenço) and therefore we are not treating this species as critically endangered. The populations from further north in the Colatina region are more susceptible to changes in the species area of occupancy due to urban expansion and farming.

ACKNOWLEDGMENTS

We would like to thank L. Kollmann, F. Saiter, and Y. Gouvêa for assistance in the field at Espírito Santo and A. J. Silva and A. Santiago at Pernambuco; Usina Frei Caneca, for the access permit at RPPN Frei Caneca; the curators and institutions of the cited herbaria; M.M. Duarte for preparing the trichome line drawings; G. Wahlert, J. Lombardi, L. Assis, L. Mentz and T.E. Almeida for suggestions and critical review. Reviews by two anonymous reviewers are greatly appreciated. This work was supported by CNPq through Process 479921/2010-5 and by the SISBIOTA program through Process 563342/2010-2 to JRS and by NSF through grant DEB-0316614 to LB. A scholarship was provided to LLG by CNPq (Process 148363/2010-5).

REFERENCES

Bohs, L. 2005. Major clades in *Solanum* based on ndhF sequence data. In: R.C. Keating, V.C. Hollowell and T.B. Croat, eds. A festschrift for William G. D'Arcy: The legacy of a taxonomist. Monogr. Syst. Bot. Missouri Bot. Gard. 104:27–49. Convention on Biological Diversity [CBD]. 2002. COP 5 Decision V/10: Global strategy for plant conservation. (www.cbd.int/decision/cop/?id=7152; accessed 16 June 2012)

CHILD, A. 1998. Studies in Solanum and related genera (6). New infrageneric taxa for the genus Solanum L. (Solanaceae). Feddes Repert. 109:407–427.

D'ARCY, W.G. 1972. Solanaceae studies II: typification of subdivisions of *Solanum*. Ann. Missouri Bot. Gard. 59:262–278. FARRUGGIA, F. AND L. BOHS. 2011. Two new South American species of *Solanum* section *Crinitum* (Solanaceae). Phytokeys 1:67–77.

FORZZA, R.C. AND 22 OTHERS. 2010. Catálogo das Plantas e Fungos do Brasil, 2 vols, Andrea Jakobsson Studio and Jardim Botânico do Rio de Janeiro, Rio de Janeiro.

GIACOMIN, L., AND J.R. STEHMANN. 2011. A new heterandrous species of *Solanum* section *Gonatotrichum* Bitter (Solanaceae) from Bahía, Brazil. Phytokeys 7:1–9.

Granados-Tochoy J.C. and C.I. Orozco. 2006. Una nueva especie de *Solanum* sección *Geminata* (Solanaceae) de Colombia. Caldasia 28:1–8.

IUCN STANDARDS AND PETITIONS SUBCOMMITTEE. 2010. Guidelines for Using the IUCN Red List Categories and Criteria. Version

- 8.0. Prepared by the Standards and Petitions Subcommittee in March 2010. http://intranet.iucn.org/webfiles/doc/ SSC/RedList/RedListGuidelines.pdf.
- KNAPP, S. 2007. Solanum coalitum (Solanaceae), a new endemic species from southern Ecuador. Novon 17:212-216.
- KNAPP, S. 2010a. Four new vining species of Solanum (Dulcamaroid clade) from montane habitats in tropical America. PLoS One 5:e10502.
- KNAPP, S. 2010b. New species of Solanum (Solanaceae) from Peru and Ecuador. Phytokeys 1:33-51.
- KNAPP, S., L. Bohs, M. Nee, and D.M. Spooner. 2004. Solanaceae: a model for linking genomics and biodiversity. Comp. Funct. Gen. 5:285–291.
- KNAPP, S. AND M. NEE. 2009. Solanum anomalostemon (Solanaceae), an endangered new species from southern Peru with unusual anther morphology. Novon 19:178–181.
- MALLET, J. 1995. A species definition for the modern synthesis. Trends Ecol. Evol. 10:294-299.
- Mentz, L.A., P.L. Oliveira, and M.V.da Silva. 2000. Tipologia dos tricomas das espécies do gênero *Solanum* (Solanaceae) na Região Sul do Brasil. Iheringia, Série Bot. 54:75–106.
- NEE, M. 1999. Synopsis of Solanum in the New World. In: M. Nee, D.E. Symon, R.N. Lester, and J.R. Jessop, eds. Solanaceae IV: Advances in Biology and Utilization, Royal Botanic Gardens, Kew. Pp. 285–333.
- NEE, M., L. Bohs, and S. Knapp. 2006. New species of *Solanum* and *Capsicum* (Solanaceae) from Bolivia, with clarification of nomenclature in some Bolivian Solanaceae. Brittonia 58:322–356.
- Peralta, I.E., D.M. Spooner, and S. Knapp. 2005 New species of wild tomatoes (Solanum section Lycopersicum: Solanaceae) from northern Peru. Syst. Bot. 30:424–434.
- ROE, K.E. 1971. Terminology of hairs in the genus Solanum. Taxon 20:501-508.
- ROE, K.E. 1972. A revision of Solanum section Brevantherum (Solanaceae). Brittonia 24:239-278.
- Stehmann, J.R., L.A. Mentz, M.F. Agra, M. Vignoli-Silva, and L.L. Giacomin. 2010. Solanaceae. In: R.C. Forzza (and 22 others), eds. Catálogo das Plantas e Fungos do Brasil, 2 vols, Jardim Botânico do Rio de Janeiro, Rio de Janeiro. Pp. 1633–1649.
- Stern, S.R. and L. Bohs. 2009. Two new species of *Solanum* from Ecuador and new combinations in *Solanum* section *Pachyphylla* (Solanaceae). J. Bot. Res. Inst. Texas 3:503–510.
- Stern, S.R. and L. Bohs. 2012. An explosive innovation: phylogenetic relationships of *Solanum* section *Gonatotrichum* (Solanaceae). PhytoKeys 8:89–98.
- STERN, S.R., L. BOHS, L.L. GIACOMIN, J.R. STEHMANN, AND S. KNAPP. 2013. A revision of *Solanum* sect. *Gonatotrichum*. Syst. Bot. 38:471–496.
- Tepe, E.J. and L. Bohs. 2009. Three new species of *Solanum* section *Herpystichum* (Solanaceae). J. Bot. Res. Inst. Texas 3:511–519.
- VORONTSOVA, M.S. AND S. KNAPP. 2012. A new species of *Solanum* (Solanaceae) from South Africa related to the cultivated eggplant. PhytoKeys 8:1–11.
- Weese, T.L. and L. Bohs. 2007. A three gene phylogeny of the genus Solanum (Solanaceae). Syst. Bot. 32:445–463.